SHORTER ARTICLES AND DISCUSSION

MODIFICATIONS OF THE 9:3:3:1 RATIO

A. Chemical Experiments Paralleling the Several Possible Modifications of the Mendelian F_2 Di-hybrid Phenotypic Non-blending Ratio 9:3:3:1

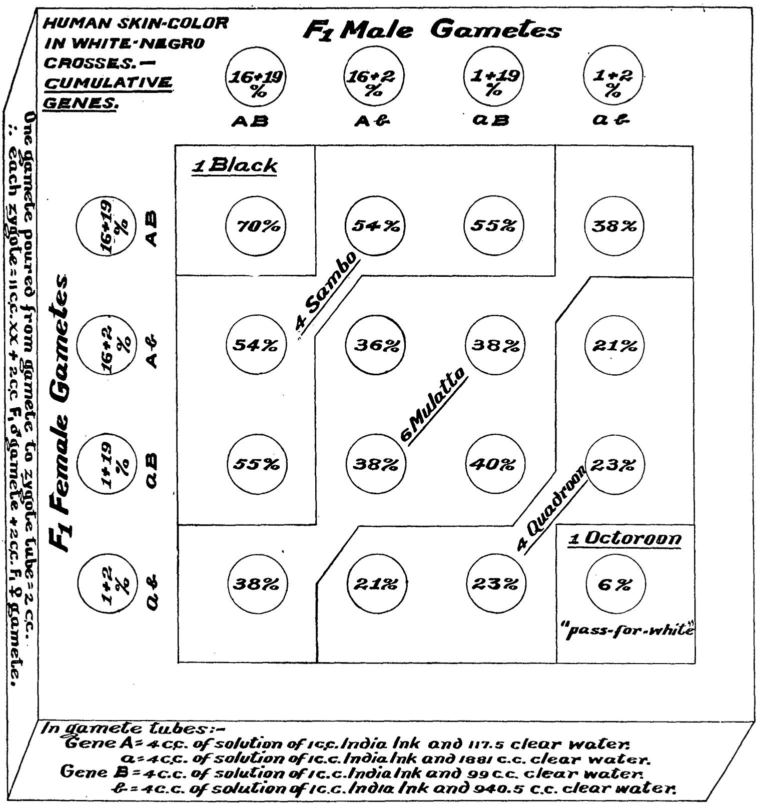
The foundation F_2 di-hybrid ratio 9:3:3:1 consists of 9 individuals having somatic traits both "A" and "B," 3 individuals having "A" only, 3 having "B" only, and 1 having neither "A" nor "B." Or, if each allelomorphic pair consists, not in a gene and its absence, but in genic entities contrasted in quality or quantity and showing clean-cut dominance and recessiveness, in 9 "A" and "B" both dominant; 3 "A" dominant, "b" recessive; 3 "a" recessive, "B" dominant; 1 "a" and "b" both recessive. This di-hybrid ratio was one of the early discoveries of Mendel[1] himself, but after the revival of genetical studies in 1900 experimental breeding had not continued long before modifications of this ratio became apparent. Thus Bateson[2] mentions a number of cases in which the 9:3:4 F_2 ratio is found. It is apparent in such cases that two unit trait-pairs are involved, that the dominant phase of one of them standing without that of the other in 3 individual F_2 somas is not to all patent aspects different from the 1 individual possessing the dominant phase of neither of the two trait-pairs involved. In the gametes of individuals of families that produce the 9:3:4 ratio the segregation and recombination of genes are, however, just as clean-cut and follow the same rule as in pedigrees giving the unmodified foundation ratio 9:3:3:1; only the somatic working out of the genes is different in the two ratios.

Barring blending, linkage, crossing-over, non-disjunction, sex-limited inheritance and other special phenomena, which limitations preserve intact the numerical entities 9, 3, 3, and 1, the

1 Mendel, G., "Experiments in Plant Hybridization" (reprinted in English in Bateson's "Mendel's Principles of Heredity," pp. 334–379), p. 351, 1866.

2 Bateson, W., "Mendel's Principles of Heredity," p. 80, 1913.

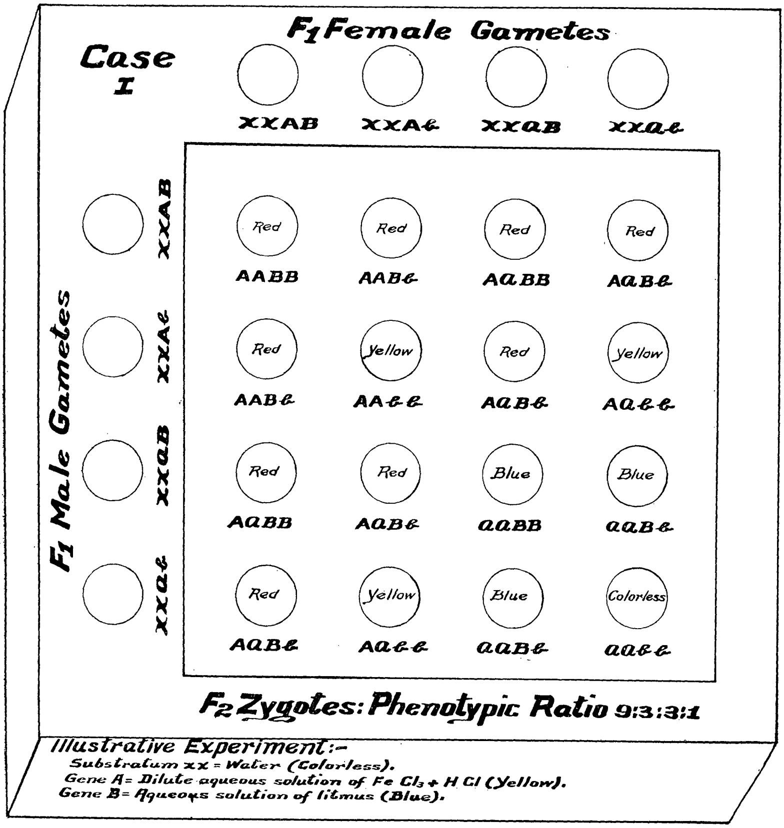
Experiment Illustrative of Black Skin-Pigment Inheritance:—
Substratum xx = 11 c.c. clear water in each of the 16 zygote tubes.



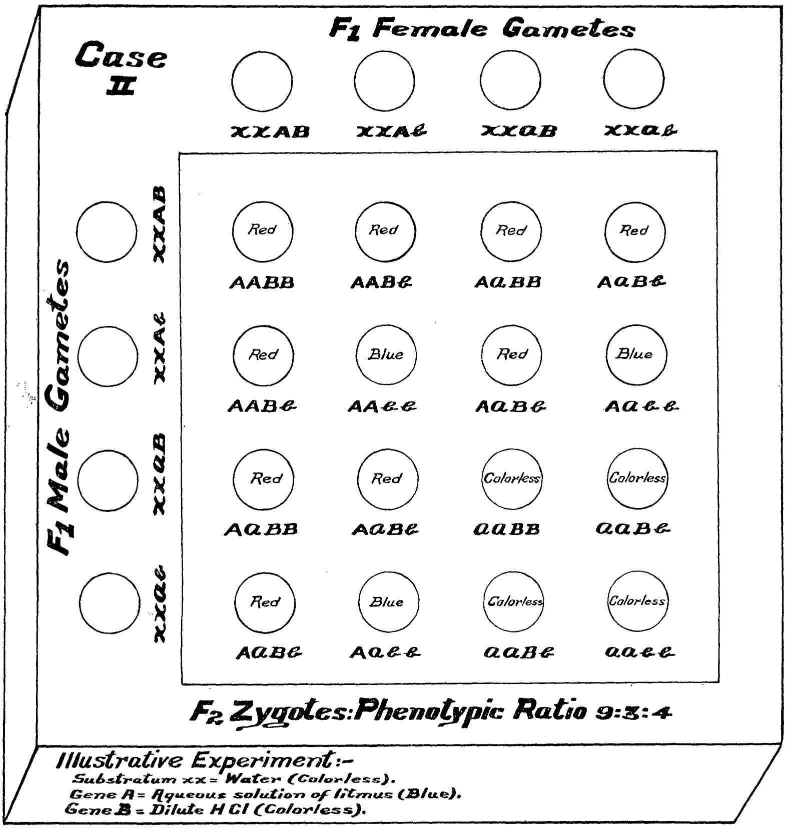
following table presents in orderly fashion all of their possible ratio-recombinations:

Series A

Case	I.	9:3:3:1.
Case	II.	9:3:4.
Case	III.	9:6:1.
Case	IV.	9:7.
Case	V.	10:3:3.
Case	VI.	10:6.
Case	VII.	12:3:1.
Case	VIII.	12:4.
Case	IX.	13:3.
Case	X.	15:1.

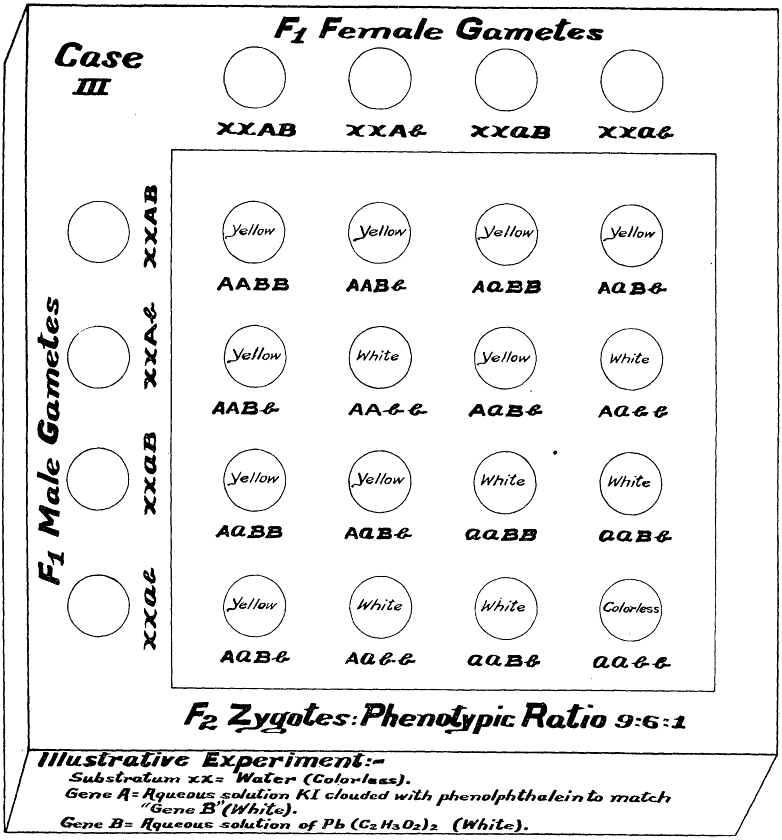


The chemical experiments described in the accompanying figures parallel chemically what must happen to the F_1 genes in their development into traits in the F_2 somas in each case of a modified somatic di-hybrid ratio. Each drawing represents a 2-inch wooden block $7\frac{1}{2}$ inches square, with twenty-four $\frac{5}{8}$-inch holes, $1\frac{1}{4}$ inches deep, suitable for holding test-tubes. The four holes at the top hold test-tubes containing chemicals representing the four types of F_1 female gametes possible when di-hybridism is being considered; the four to the left perform the same service for the four male gametes. The sixteen holes blocked off in the square hold test-tubes for the sixteen types of zygotes resulting, by the checker-board method, from all possible unions of the four male and the four female gametes. X X represent the substratum or the sum-total of hereditary qualities other than the traits under consideration. The lettering under each test-tube circle is the genetic formula for the gamete, or zygote as the



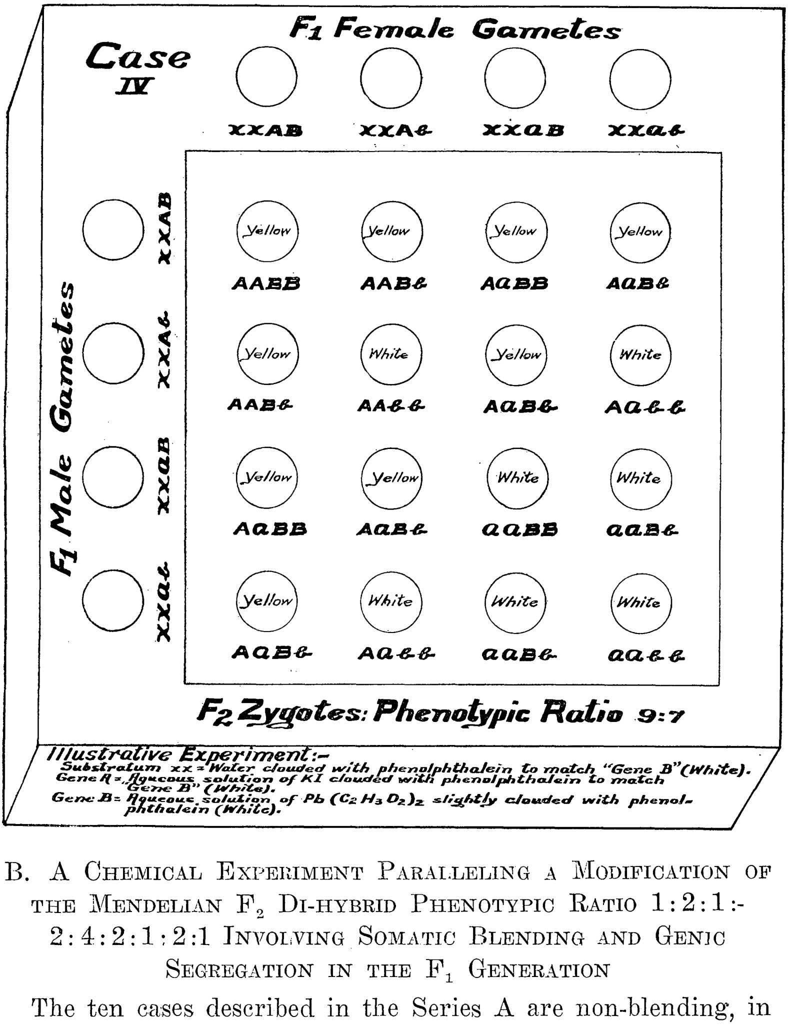
case may be. A word within a test-tube circle names the color of the reaction-product, which color is the index or analog of the somatic working out of its accompanying genetic formula of the soma.

Instructions for performing the experiment illustrative of each ratio-modification are found in detail in the drawing for the selected case. The chemicals representing gene "A" and gene "B" and the substratum are, as indicated, poured into the test-tubes representing the F_1 female and the F_1 male gametes. Each gamete-holding test-tube should contain approximately 20 c.c. of the appropriate genes and substratum. Of this mixture 4 c.c. represent 1 gamete; and 1 such gamete is to be poured into each one of the 4 zygote-holding test-tubes, directly below or directly to the right, as the case may be, of particular gamete-holding test-tube, following the checker-board method. Thus each of the 16 zygote test-tubes will contain chemicals appro-



priately representing 1 F_1 male and 1 F_1 female gamete free, like the constituents of a united sperm and egg, to interact in the zygote and in subsequent ontogenesis.

Some of these ratios, such as exist in Cases Nos. V, VI and IX, are much more difficult chemically to contrive than others, such as Nos. I, II, III, IV and X. It is not surprising, then, that nature provides more readily cases in inheritance representing the latter ratios, while the former are being found only by the most diligent genetical study. Not all of these ratios have yet been found in nature by experimental breeding, but, from time to time, a geneticist reports the discovery of a new di-hybrid F_2 ratio which proves to be a member of this series. Doubtless all of them will be found in time, but without introducing the special phenomena earlier referred to, Series A, consisting of 10 cases, exhausts the possibilities of F_2 phenotypic dihybrid ratios.

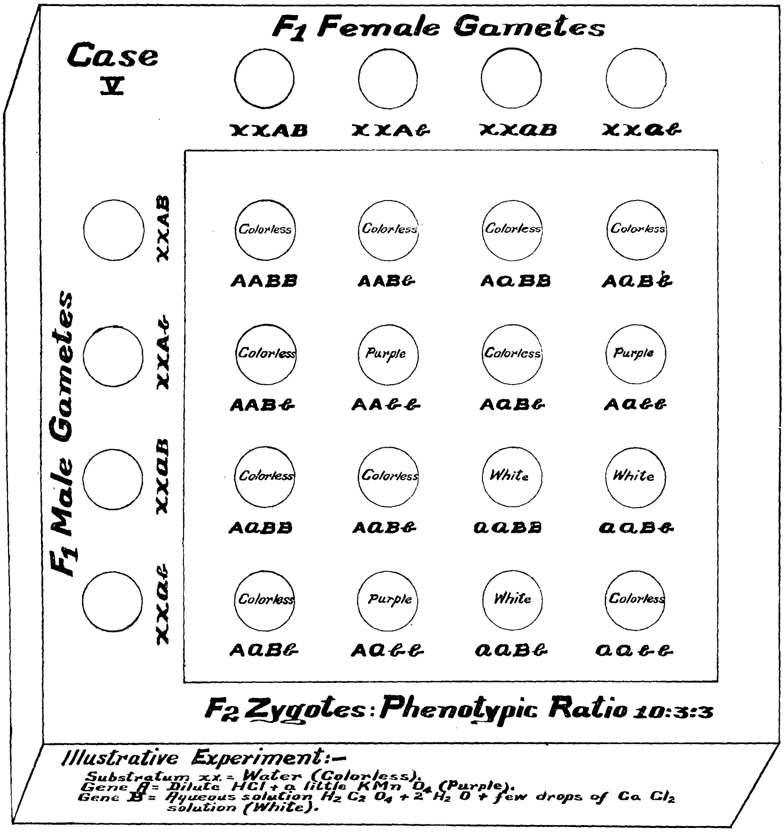


B. A Chemical Experiment Paralleling a Modification of the Mendelian F_2 Di-hybrid Phenotypic Ratio 1:2:1:2:4:2:1:2:1 Involving Somatic Blending and Genic Segregation in the F_1 Generation

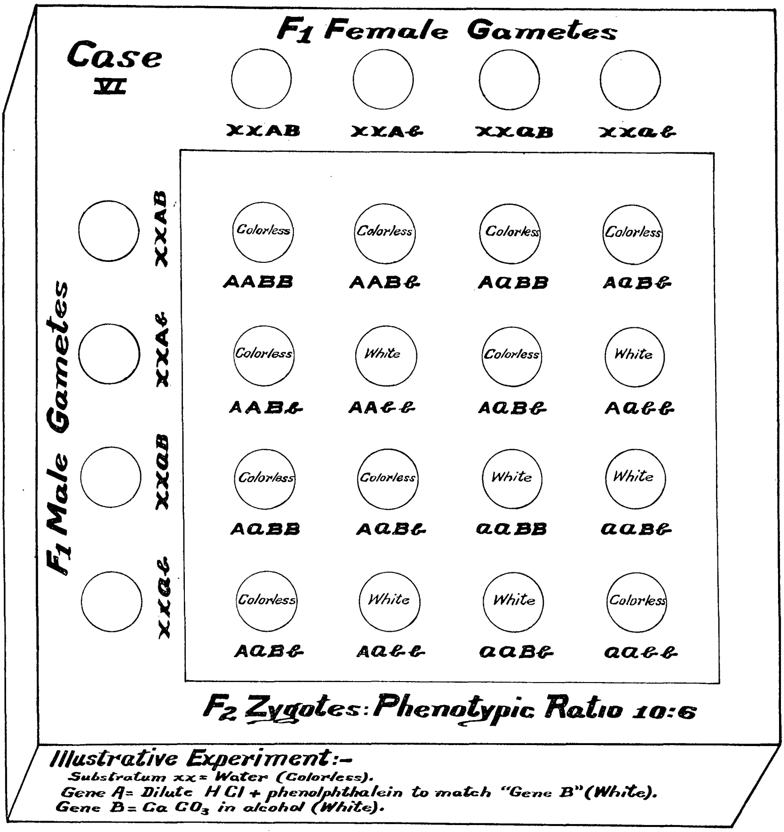
The ten cases described in the Series A are non-blending, in which the entities 9, 3, 3, and 1 are kept intact, that is, they are simply recombined. The mono-hybrid ratio on which they are based is the normal dominant-recessive 3:1 relation. The typical blending ratio in the F_2 mono-hybrid is 1:2:1. Carrying this latter ratio into the di-hybrid classification in the same manner as the 3:1 ratio was carried into the 9:3:3:1 classification gives us the following: 1:2:1:2:4:2:1:2:1, a total of sixteen individuals divided into 9 classes.

In Davenport's[3] study on the "Inheritance of Skin-Color in

[3] Davenport, C. B., "Skin-Color in Negro-White Crosses," Pub. 188 Car. Inst. Wash., 1913.

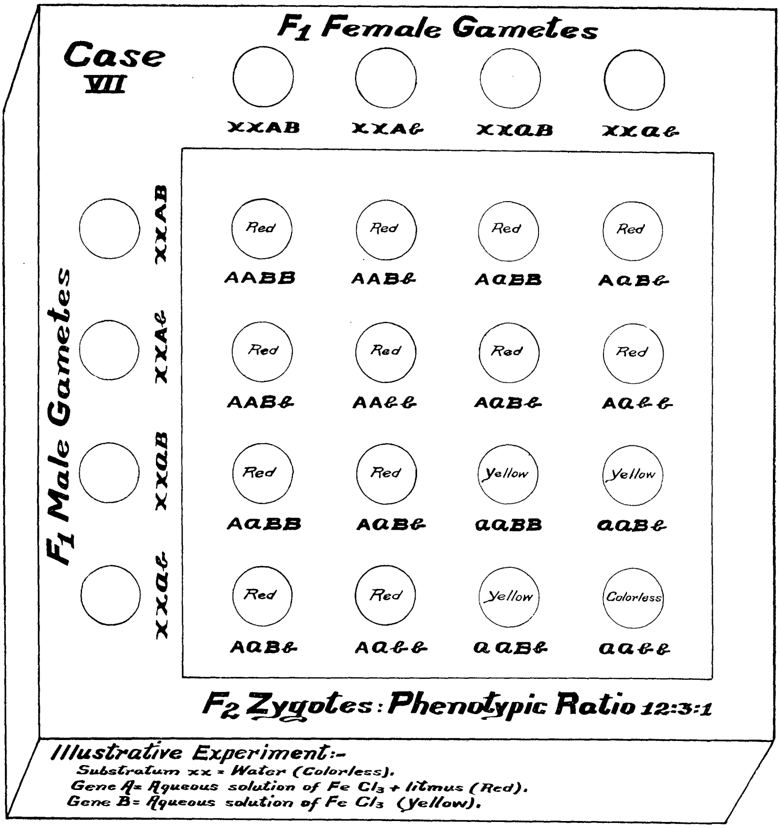


Negro-White Crosses'' he found that the amount of black skin-pigment in an individual is determined by two genes in each parental gamete, and in measuring the intensity of black skin-pigment in the members of a great many highly hybridized families he found 5 definite maxima in the curve plotting the distribution of individuals according to the per cent. of black skin-pigment carried. Theoretically (unless genes ''A'' and ''B'' are exactly equally potent in developing into a definite per cent. of blackness showing in the unweathered skin) there should have been 9 maxima in the above-described distribution curve. Arbitrarily giving the genes the following potentiality for somatic expression, ''A'' 16 per cent., ''B'' 19 per cent., ''a'' 1 per cent., ''b'' 2 per cent. (which is not far from the the facts of the case), the somatic frequencies and black skin-color percentages would run as follows: One 70 per cent., two 54 per cent., one 36 per cent., two 55 per cent., four 38 per cent.,



two 21 per cent., one 40 per cent., two 23 per cent., and one 6 per cent., in a total of 16 individuals.

But practically 5 instead of 9 somatic types were actually found because gene "A" and gene "B" are so nearly equal in value that it is not possible in a given individual, simply by measuring the skin-color pigment, to determine whether gene "A" or gene "B" is responsible for the quantity of melanin possessed. Thus in the 5 classes the two 54 per cent. cases (AABb) and the two 55 per cent. cases (AaBB) constitute the three quarters blacks or "sambos," the two 21 per cent. (Aabb) cases and the two 23 per cent. (aaBb) cases constitute the one quarter blacks or "quadroons," while the one 36 per cent. (AAbb) case and the one 40 per cent. (aaBB) case are so nearly like the four 38 per cent. (*i. e.*, the "mulatto" AaBb) that they constitute a single class of six individuals. Hence the contracted ratio 1:4:6:4:1.

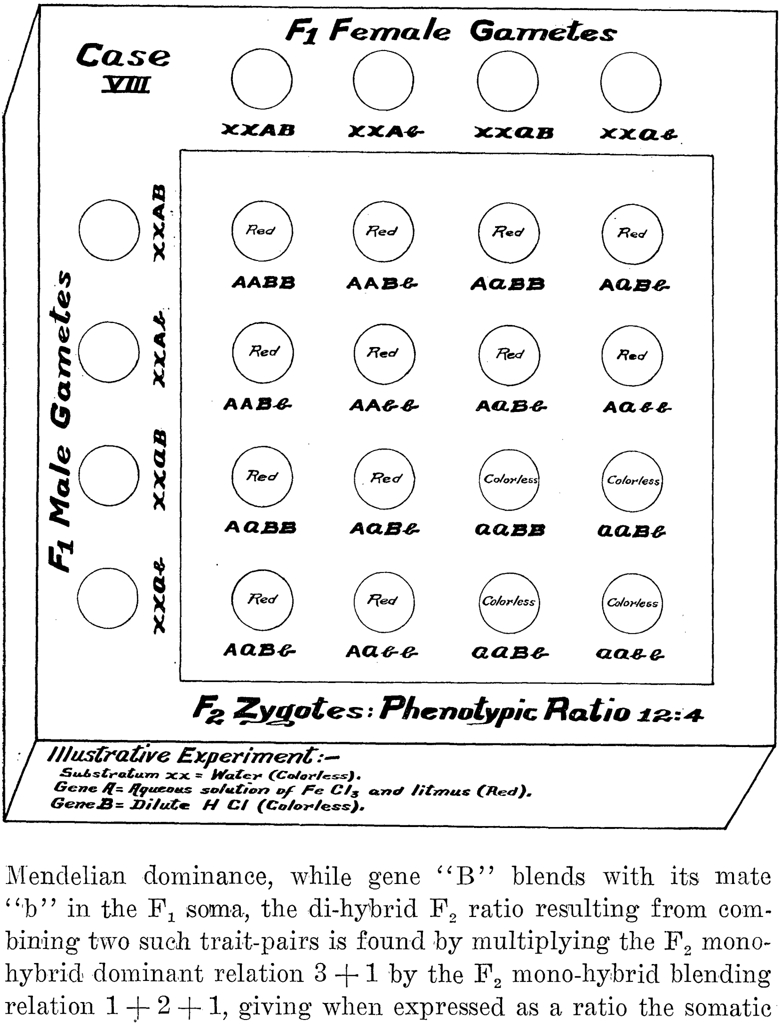


As Davenport clearly points out in the matter of black skin-pigment, each gene finds its definite somatic expression regardless of the presence of other genes. Since the two genes work out into the same somatic trait (*i. e.*, are duplicate genes) which somatic expressions differ only in quantity, they might well be be called cumulative genes. The accompanying diagram (Experiment Illustrative of Black Skin-Pigment Inheritance) gives specific directions for running this experiment in a manner very closely paralleling what Davenport found in nature.

This experiment illustrates only one case in a long possible series of modifications of the foundation F_2 di-hybrid phenotypic blending ratio 1 : 2 : 1 : 2 : 4 : 2 : 1 : 2 :1.

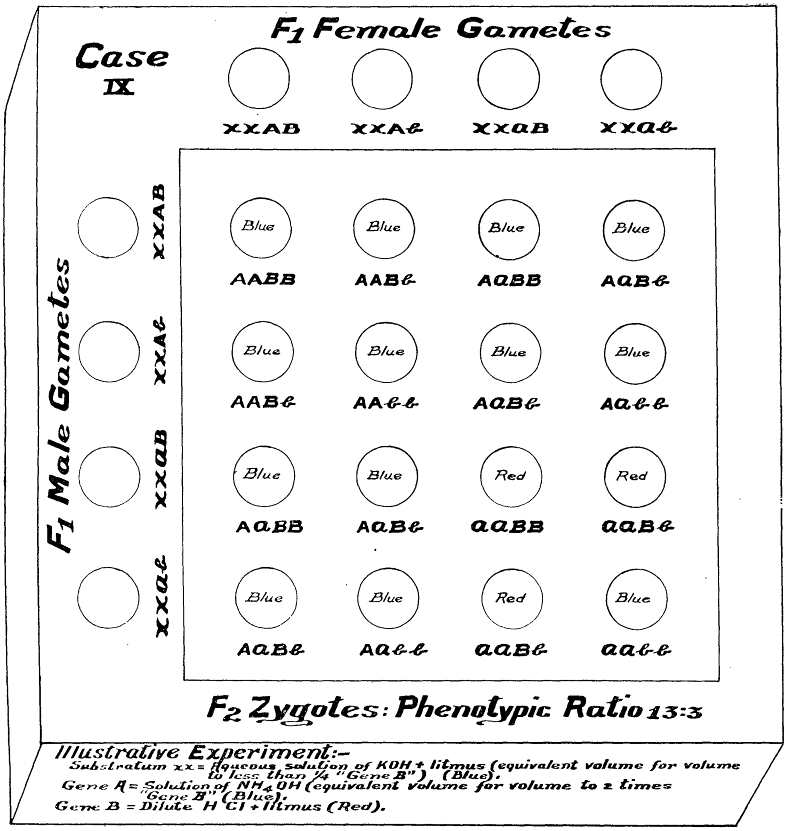
C. Other F_2 Di-Hybrid Series

In a case in which gene "A" does not blend with its allelomorphic mate "a" in the F_1 soma, but presents a typical case of

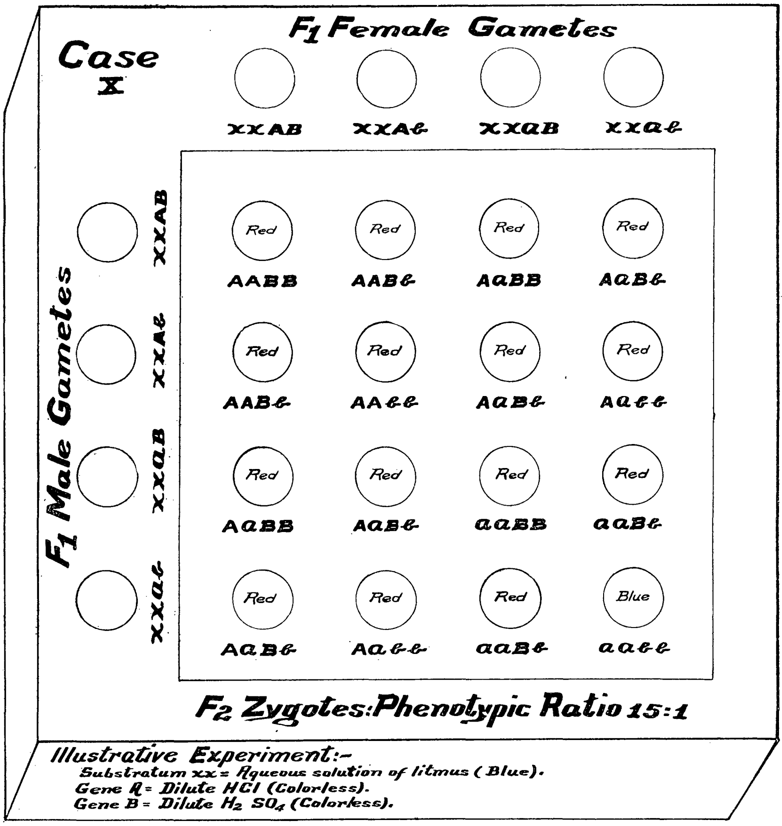


Mendelian dominance, while gene "B" blends with its mate "b" in the F_1 soma, the di-hybrid F_2 ratio resulting from combining two such trait-pairs is found by multiplying the F_2 mono-hybrid dominant relation $3 + 1$ by the F_2 mono-hybrid blending relation $1 + 2 + 1$, giving when expressed as a ratio the somatic F_2 di-hybrid relation $3:6:3:1:2:1$. Among other special cases to be considered are those involving crossing-over, non-disjunction and sex-limited inheritance.

When the genic and somatic specifications of a ratio are known it is not difficult to contrive a chemical parallel for it. The use of such experiments consists not only in clarifying the conception of the particular situation at hand, but also in providing in the laboratory a nearer approach than is usually used for demonstration to what is actually happening in heredity. The chemical analogy between what happens in the zygote-holding test-tube and what actually happens in the somatic working out of the



segregable genes in the members of the F_2 ratios is doubtless much closer than any completely mechanical contrivance can show. In the experiments the blending quite properly is shown complete in the zygote and soma, but if the analogy were carried still further one should be able to dip into the gamete-holding test-tubes and there find that some of the original F_1 genes remain unchanged—the unchanged germ-plasm which is left behind—and to lift out well-defined gametes with "A" or "a" and "B" or "b" variously combined, according to the constituent genes of the zygote, for in the living germ-cell cycle, not the blending of the soma, but clean-cut segregation is the rule. Representing the gametes by capsules containing genes in solid form, which capsules and genes would be slowly soluble in the substratum of the zygote, would drive the analogy a little closer to nature.



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COLD SPRING HARBOR H. H. LAUGHLIN.

THE FACTORS FOR YELLOW IN MICE AND NOTCH IN DROSOPHILA

IN a recent number of THE AMERICAN NATURALIST[1] appeared a paper by Ibsen and Steigleder on "Evidence for the Death in Utero of the Homozygous Yellow Mouse." In summing up (p. 751), after stating that "our evidence tends to confirm the conclusion of Castle and Little that in mice homozygous yellow zygotes are produced in the yellow × yellow mating, but that these

[1] Vol. LI, No. 612, December, 1917, pp. 740–752.